A NEW ARTICULATED THELODONT (AGNATHA) FROM THE EARLY DEVONIAN OF BRITAIN

by SUSAN TURNER

ABSTRACT. A new articulated early Devonian specimen of a thelodont from Britain is described. It is a nikoliviid and is referred to a new species, *Nikolivia milesi*. The scales of this form bear some resemblance to those of *N. oervigi* (Karatajute-Talimaa 1968) and *N. elongata* (Karatajute-Talimaa 1978), and possibly *N.*? ('*Sigurdia*') *heintzae* (Dineley and Loeffler 1976). The presence of a possible pore canal system is noted. No other new characters to help decide the relationship of thelodonts to other agnatha are present. A comparison is made with other articulated thelodonts and a suggestion for the mode of life is given.

IN August 1933 and June 1934 Dr. E. I. White and Mr. H. A. Toombs collected a suite of early Devonian fishes from Wayne Herbert Quarry, near Newton, Herefordshire (fossils housed in the British Museum (Natural History)). From a green siltstone lenticle and contiguous beds they obtained remarkably complete pteraspids (White 1935), several cephalaspids, as yet undescribed, and acanthodians (Miles 1973). In searching the collection for acanthodian remains in 1971 Dr. Roger Miles noticed on the underside of a slab a patch of scales which were not acanthodian. This specimen, which may have been overlooked because it is obvious only under oblique or subdued lighting, was shown to the author, who confirmed that it was a thelodont.

Articulated thelodonts are rare; most of the fifty to sixty thelodont species described are known from isolated scales. Only two articulated specimens (Pl. 97) and a small patch of scales, all of *Turinia pagei*, have been reported from the Lower Devonian of Britain: from Scotland (Traquair 1899; Ørvig 1969) and Gloucestershire (Allen, Halstead (Tarlo) and Turner 1968). From a preliminary examination I suspected that the Wayne Herbert thelodont might also be *T. pagei*, but further study of a cast of the natural mould reveals that it is a new species of *Nikolivia* (Family Nikoliviidae). Descriptions of nikoliviids have hitherto been based on isolated scales from the early Devonian of Europe (Karatajute-Talimaa 1968, 1978; Turner 1973). Articulated material from Canada, referred to *Sigurdia heintzae*, and undetermined scales figured by Dineley and Loeffler (1976, pl. 22, figs. 65, 66) are considered to belong to this family.

SYSTEMATIC PALAEONTOLOGY

Order THELODONTIDA
Family NIKOLIVIIDAE Karatajute-Talimaa, 1978
Genus NIKOLIVIA Karatajute-Talimaa, 1978

Diagnosis. Small to large thelodonts with triangular pectoral flaps flanking a large cephalothorax, and trunk covered with imbricated scales with some areas of non-imbricated scales. More robust and elongate large scales along the leading edge of the pectoral flaps. For detailed diagnosis of the scales see Karatajute-Talimaa (1978, p. 140).

Type species. *Nikolivia oervigi* (Karatajute-Talimaa, 1968).

Other species. *N. balabayi* Karatajute-Talimaa, 1978; *N. elongata* Karatajute-Talimaa, 1978; *N. gutta* Karatajute-Talimaa, 1978; *N.*? *heintzae* (Dineley and Loeffler, 1976); *N.* sp. (*Apalolepis toombsi pars* Turner, 1973).

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Nikolivia milesi sp. nov.

Text-figs. 1–5.

1972 new articulated thelodont; Turner (1972) p. 18.

Derivation of name. In honour of Dr. R. S. Miles, who recognized the type specimen.

Diagnosis. Large thelodont (in excess of 145 mm). Cephalothorax long with slim triangular pectoral flaps, posterior to which body narrows. Scales average length 1·5 mm with thin lanceolate and leaf-like crowns. Body scale crowns with slightly raised, narrow, grooved central ridge with long posterior spur and one-to-three lateral ridges or steps leading to shorter posterior points. Large lanceolate scales, average size 2 mm along leading edge of flaps and at least part of lateral rim of body. These scales flat-topped, some with a side rib. Small areas of long asymmetrical or subrectangular scales, some possibly with pores, part of a sensory-line system. Elliptical bases with pulp cavity reduced to a slit in older scales.

Holotype. Articulated scales, BMNH P. 53902.

Other material. A smaller patch of scales (P. 58216), approximately 85 × 50 mm, is interpreted as a pectoral flap and part of the thorax and abdomen just posterior to the flap. This specimen was on the underside of a slab with *Pteraspis rostrata* (P. 17526I). A patch of articulated scales alongside the holotype of acanthodian *Uraniacanthus spinosus* Miles, 1973 (P. 16609, pl. 11), may also belong to *N. milesi* (only examined from the photograph).

Horizon and locality. Ditton Series, about 66 m above the main 'Psammosteus Limestone', *Pteraspis crouchi* Zone, Early Devonian, Wayne Herbert Quarry, south-west Hereford and Worcester. (N.B. This is an SSSI monitored by the Nature Conservancy Council.)

Description. The type specimen is preserved as a natural mould in fine-grained sediment. The dimensions of the scale area are about 145 mm along the antero-posterior axis by 60 mm across the widest part.

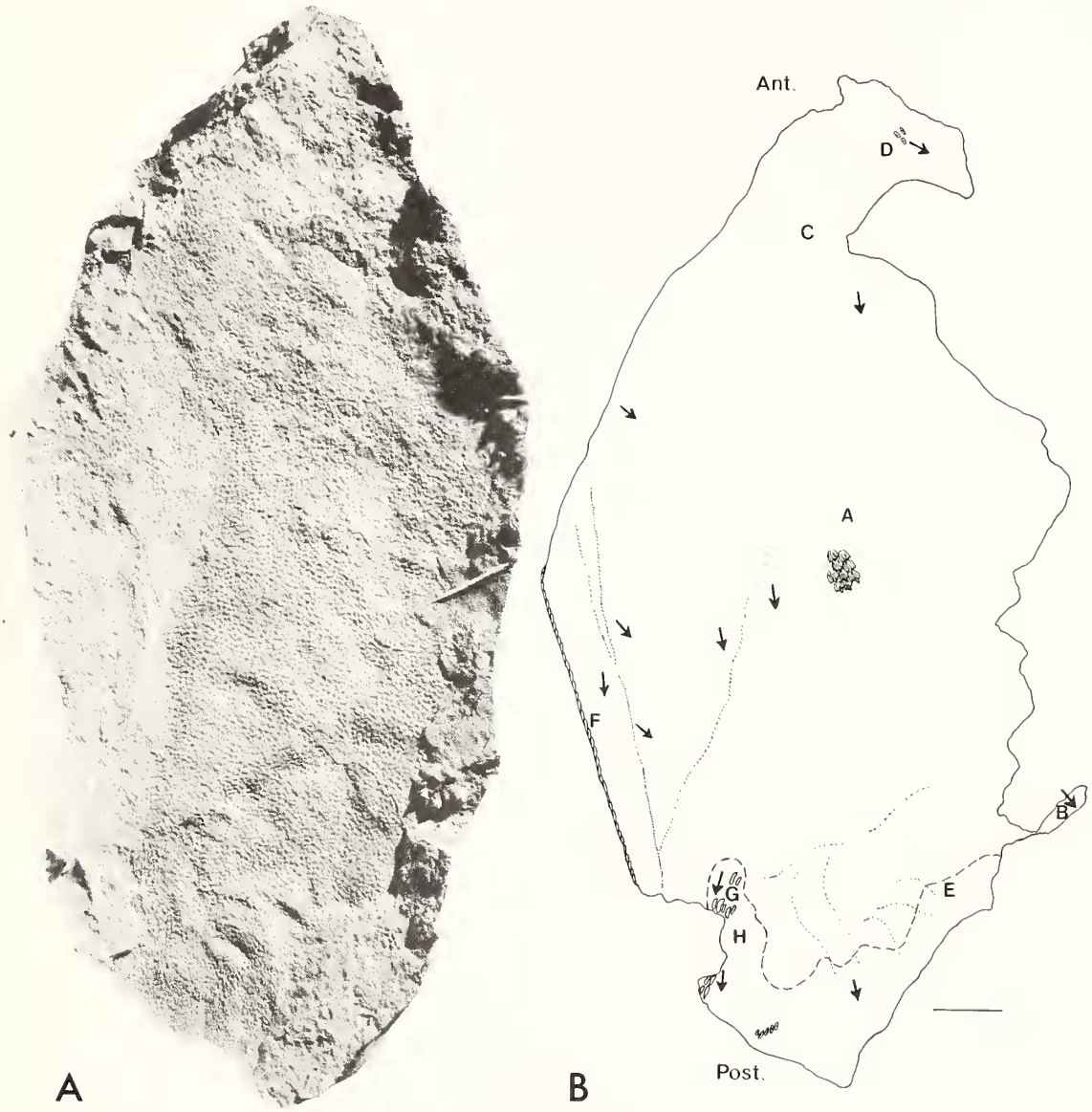
General outline and scale orientation are shown in text-fig. 1. A rough estimate of the scale count in this area is 5000. The only evidence of a natural margin is on the mid-to-lower left side, where the shagreen turns into the rock at about 80°. Here there is a strip of scales the distal edge of which appears to be the rim of the body. This strip tapers posteriorly and ends where the rock is broken (see text-figs. 1, 3). On the inner side of the inturned strip is a marked groove, a fold in the squamation; proximal to this a slight fold passes medially at an angle of about 45°, and fades out anteriorly. There are no other obvious surface features except for shallow ripples.

Over most of the area the typical nikoliviid body scales are partially imbricated, the dentate posterior crown edges just overlapping the anterior edges of the scales behind (see text-figs. 2A, 4). Except for two places the scales are all seen in crown view. Only at the front and in a semicircle near the posterior rim are some preserved base upwards (see text-fig. 1); there they appear to be more lanceolate and possibly not imbricated (text-fig. 2E). On the natural rim the scales can be seen crowded together and in lateral view (text-figs. 2F, 3).

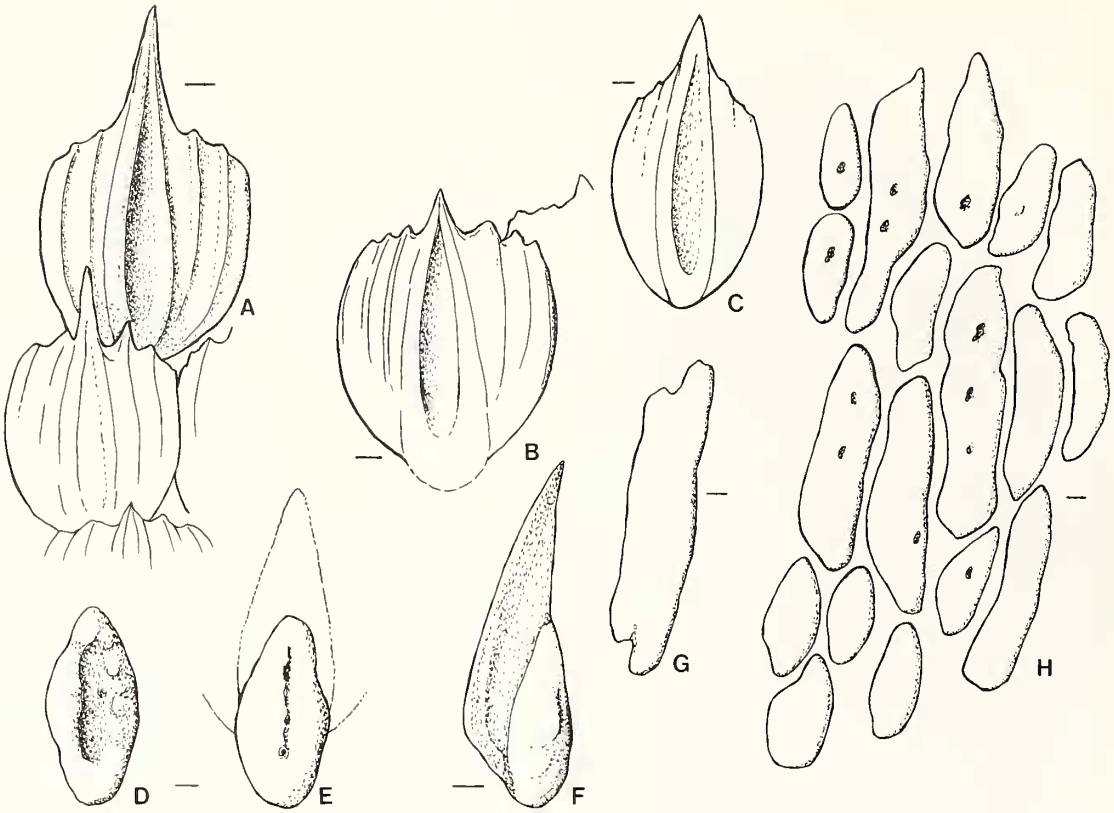
Towards the back on both sides, but clearly on the left, are small areas of atypical scales. These are long, elliptical or subrectangular non-imbricate scales, flanked by typical body scales (see text-figs. 2G, H, 5). In some of these atypical scales there are small depressions or pores which do not appear to be pulp openings (text-fig. 2H). Some of the bases appear to have small thickened nodes around the pulp cavity (text-fig. 2D).

As no scales are preserved other than as impressions no thin section could be made, though from the general form the scales are probably of *Thelodus*-type histology (see Gross 1967) and similar to other nikoliviid scales (see Karatajute-Talimaa 1978).

Discussion. From the evidence of the scale form the Wayne Herbert thelodont is a new species of nikoliviid. Only one scale of *N. oervigi* figured by Karatajute-Talimaa (1978, pl. XLVI, fig. 6*a*) resembles those of *N. milesi.* In fact the crown shapes of this new form look more like those of



TEXT-FIG. 1. *Nikolivia milesi* sp. nov. A, cast of BMNH P. 53902, Early Devonian, Ditton Series, Wayne Herbert Quarry, Hereford and Worcester. B, outline diagram of preserved shagreen. Arrows show scale elongation and anterior to top. Posterior to dashed line most scales appear to be preserved in basal view. Letters mark sites of scales seen in text-figs. 2–5. (Scale line = 1 cm.)



TEXT-FIG. 2. *Nikolivia nilesi* sp. nov. A, body scales in crown view showing imbrication. B, body scale in crown view. C, transitional? scale in crown view. D, base of anterior scale. E, base of posterior body scale. F, pectoral flap rim scale in lateral view. G, asymmetrical scale. H, group of asymmetrical scales, showing pores or highly constricted pulp openings. (Scale lines = 0·1 mm.) All from BMNH P. 53902.

Apalolepis; scales of this genus were described by Karatajute-Talimaa (1968, 1978) and Turner (1973). They have a high neck and trumpet-shaped base and differ from nikoliviids with a low-necked base. The scales of *N. milesi* seen in basal and lateral view are similar to those of *N. elongata* and some described as *T.*? *oervigi* by Turner (1973), but unfortunately their crown surfaces are obscured. The scales on the natural margin, however, do appear simpler in outline than the striated body scales (see text-fig. 3).

To date no isolated scales have been extracted from Wayne Herbert rocks, and only a few nikoliviid and apalolepidid scales have been found from other localities in England that could be

EXPLANATION OF PLATE 97

Figs. 1–3. *Turinia pagei* (Powrie). Holotype (RSM 1891.92.133). Lower Old Red Sandstone, Lower Garvock Group, Turin Hill, Angus, Scotland. 1, whole specimen × ⅔. 2, branchial and pectoral area to show scale sizes and distribution, × 1 approx. 3, pectoral flap to show scale differentiation and fining of scales on trailing edge, × 1 approx.

1

2

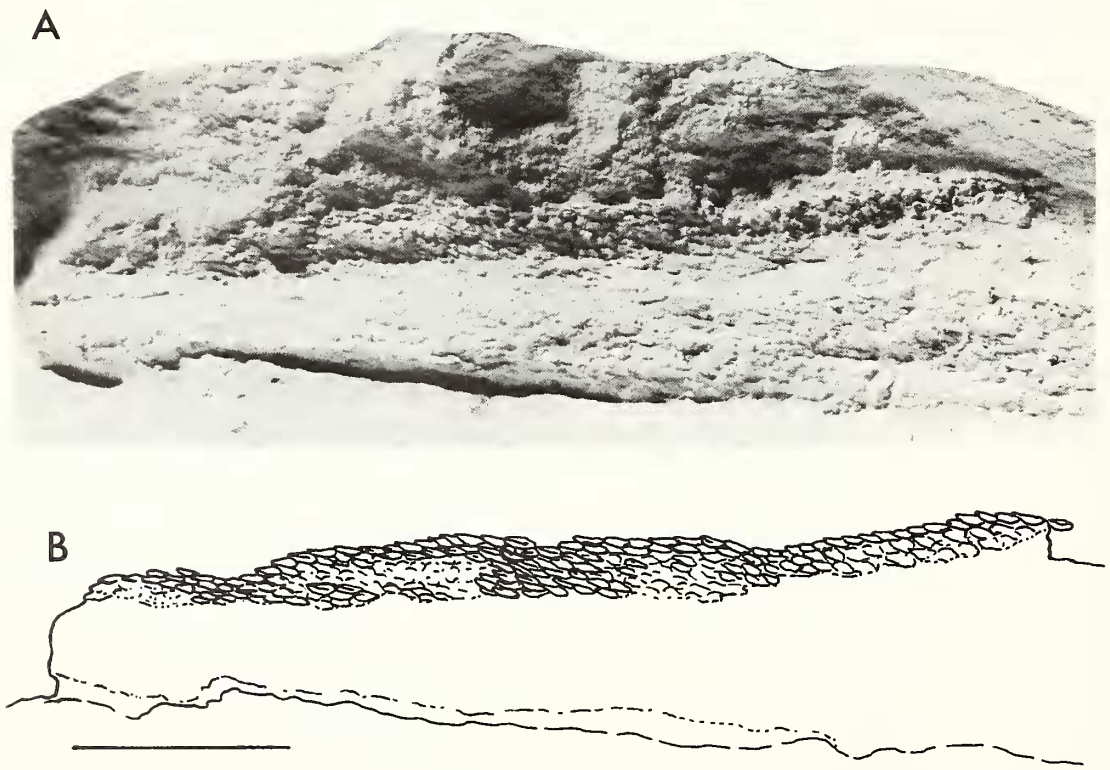
3

TURNER, Early Devonian thelodont

compared with *N. milesi*. Karatajute-Talimaa (1978, p. 129) referred the scales of *A. toombsi* Turner, 1973 to the genus *Nikolivia*. This is accepted in part. However, some of the Welsh Borderland scales are closer to *Apalolepis*, having the high-necked bases, but as so few have yet been found it has not been possible to make a complete histological study. None of the *toombsi* scale forms resemble those of *N. milesi*. The scales of *T.? oervigi* from the Welsh Borderland (Turner 1973) fall into the range of *N. oervigi*, *N. elongata*, and *N. balabayi*. It seems feasible that *N. milesi* is closely related to one or more of these, but because of its unusual asymmetrical scale features it is considered to warrant species status.

Comparison with other articulated thelodonts. The pectoral flap does seem to be present in *N. milesi*, preserved as the lateral strip of scales. It is somewhat folded but appears long and narrow, unless the diagonal fold in the main squamation was caused by the rest of the pectoral flap being tucked under during burial. The presence of closely packed, more robust scales on the leading edge of the pectoral fin appears to be a common feature in thelodonts. Usually there are loosely packed, finer and smaller scales on the trailing edge, allowing more flexibility. This is well shown in the holotype *Turinia* (Pl. 97, fig. 3); this edge is obscured in *N. milesi*.

Another thelodont, called *S. heintzae* by Dineley and Loeffler (1976) has large scales along the pectoral flap and also apparently along the body margin as seen flattened dorso-ventrally. Closer examination of these Canadian specimens being undertaken by Dr. Loeffler, Dr. Goujet, and myself confirms that this is a nikoliviid with very similar scale morphology to, although a smaller form than, *N. milesi*. The use of the genus-name *Sigurdia* (Heintz 1972), based as it was upon an impression in



TEXT-FIG. 3. *Nikolivia milesi* sp. nov. A, strip of scales thought to represent the pectoral fin, ×3 approx. B, diagram of strip to show crowded rim scales at site F. (Scale line = 1 cm.)

sandstone from Spitsbergen and thought to be thelodont, despite the lack of scales, should be discontinued.

N. milesi also has structures in common with *Phlebolepis elegans* Pander (see e.g. Ritchie 1968). *Phlebolepis* has a dermal armour of thin, imbricated, ribbed scales, with asymmetrical scales in special areas, and pores through certain scales. This last feature Gross (1968) interpreted as a sensory-line system. The presence of pores in the elongate scales of *N. milesi* may indicate that it too possessed such a system. The region of pore scales, just posterior to the lateral flap, is comparable to that in *P. elegans* (Märss 1979). The similarities between the Silurian *Phlebolepis* and *Nikolivia* do not necessarily signify close relationship because the two forms have scales of different histological structure, *Phlebolepis* being of *Katoporus* type (Gross 1967), although the significance of this dichotomy in thelodont scale structure for phylogenetic relationships is not yet understood.

The criteria for deciding the 'way up' in articulated thelodonts are few. The studies of Kiaer and Heintz (1932) and Ritchie (1963, 1968) have shown that thelodonts had a dorsal and an anal fin and a reversed heterocercal or hypocercal tail; these are helpful indicators if preserved. However, in the absence of these fins it is not easy to be definite. If the specimen of *N. milesi* is structurally on the lower side of the rock then the ventral surface is uppermost. Scales are seen in dorsal (crown) and ventral (basal) view on the same plane, a common occurrence in thelodonts flattened dorso-ventrally. This can be seen in articulated *T. pagei* specimens in the areas where there is no infilling by sediment.

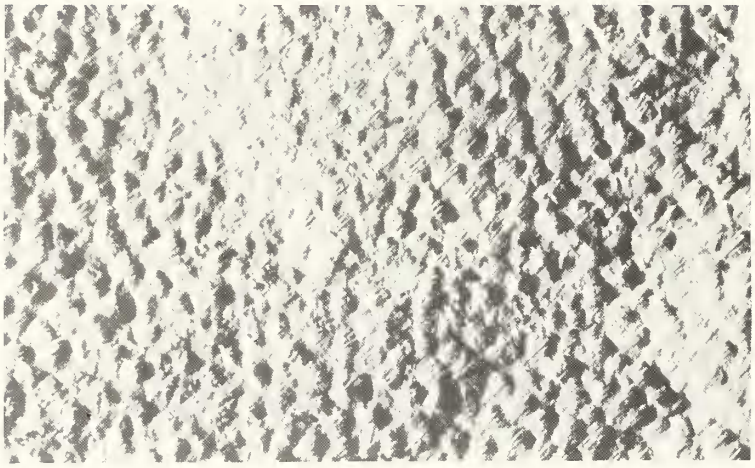
Traquair (1899, p. 599) thought the holotype *Turinia* was in dorsal view because it was 'conclusively shown by the position of the lower lobe of the heterocercal caudal fin'. If all thelodonts have a hypocercal tail, as seems possible from Ritchie's studies, then Traquair's statement is not upheld (see also Kemna 1903). Stensiö (1958, 1964) interpreted *T. pagei* as a heterostracan shown in dorsal view with nine pairs of branchial arches and extrabranchial atria, and impressions of the brain. His separation of *Turinia* from other thelodonts, particularly the family Thelodontidae, is not warranted as *T. pagei* scales are certainly no different histologically from those of the *Thelodus* group, as shown by Gross (1967). *T. pagei* has a general morphology in common with all articulated thelodonts; large cephalothorax with lateral triangular pectoral flaps, slim trunk, and armour of discrete dermal denticles. The lack of distinct orbits and nasal sacs, and the presence of what appears to be the gut region just ventral to the cephalothorax, suggest that the holotype is preserved in ventral view, as first suggested by Powrie (1870). Study of the holotype indicates only seven or eight 'branchial' arches and there is a buccal region leading from the anterior mouth into the pharynx and gut (see Pl. 97, fig. 1).

The area of the body preserved in *N. milesi* appears to coincide with that in the English *Turinia*, i.e. the ventral surface of the cephalothorax (see Allen *et al.* 1968, fig. 3), though there are no obvious branchial structures to be seen. Comparing the pectoral fin size with total length in the type *Turinia* an estimate for the length of *N. milesi* can be given as 205 mm.

In the type *Turinia* there are small patches of tiny scales distal to the branchial ridges where pectoral flap meets trunk, which may represent flaps covering branchial openings, similar to those postulated for the Scottish Silurian thelodonts (Ritchie 1968). This region is obscured by the infold and scale imbrication in *N. milesi*.

Associated Fauna

Heterostracans	*Pteraspis rostrata* var. *toombsi*
	P. rostrata var. *waynensis*
	P. rostrata var. *virgoi*
	P. jackana
	Poraspis sericea
	Weigeltaspis
Osteostracans	Several species of cephalaspids, including *Cephalaspis jacki*
Acanthodians	Climatiids: *Ptomacanthus anglicus*, *Vernicomacanthus waynensis*
	Ischnacanthid: *Uraniacanthus spinosus*
Eurypterida	*Pterygotus anglicus*?



TEXT-FIG. 4. *Nikolivia milesi* sp. nov. Body scales from site A to show imbrication of crown tips. Anterior to top right, × 60 approx.

TEXT-FIG. 5. *Nikolivia milesi* sp. nov. Asymmetrical scales from sites G and H. Posterior to top, × 60 approx.

Palaeoenvironment. All the Wayne Herbert fossils came from a green siltstone lenticle or the fine siltstone beds a few inches just above and below (H. A. Toombs, pers. comm. 1981). White (1935, p. 383) interpreted the lenticle, 50 mm thick and covering an area about 3·0 mm × 1·2 m, as a single dried-up pool in which the animals were strictly contemporaneous; Miles (1973, p. 115) agreed that these fluvial species were trapped by the drying up of the body of water in which they lived. Allen and Tarlo (1963) thought a cut-off channel had dried out. The presence of a partially complete thelodont verifies the rapid nature of the event, for presumably, unless buried quickly, thelodonts disintegrated rapidly after death, releasing thousands of scales into the surrounds. The way the pectoral flap is folded suggests it was pressed down into soft bottom sediment, which may indicate the fish were trapped in wet mud. No sedimentary structures of complete drying out have been described, and the fish, although a little disarticulated, are not contorted.

The similarities between *N. milesi*, *Phlebolepis elegans*, an inhabitant of quiet lagoons (Märss and Einasto 1978), and *N.? heintzae*, also interpreted as a quiet lagoonal or hyposaline form (Dineley and Loeffler 1976), suggest that the English form also lived in quiet water, such as the ephemeral ponds and lakes of the early Devonian Welsh Borderland floodplain (Allen and Tarlo 1963). The nikoliviids are apparently rare in British samples, whereas *Turinia* scales are common. Does this mean that the more fragile nikoliviid scales behaved differently as sedimentary particles or that the fish preferred different environments, *Turinia* perhaps being more adapted to bottom living in faster-flowing rivers and streams?

There are at least two large predators in the fauna, the acanthodians, one of which had apparently swallowed or was in the process of swallowing a small cephalaspid (Miles 1973, pl. 1, fig. 2), and eurypterids, both of which may have regarded thelodonts as prey.

Stratigraphical significance. The nikoliviids now seem to be an integral part of the early Devonian thelodont fauna in Europe. They are found often in association with turiniids (Karatajute-Talimaa 1978; Turner 1973). The presence of nikoliviids in North-West Canada in rocks of Late Silurian or early Devonian age (Dineley and Loeffler 1976; Vieth 1980) also indicates the close links between North America and Europe at this time. Recently they have been found in younger Devonian rocks in Australia associated with turiniids (Turner and Dring 1981; Turner, Jones and Draper 1981).

Geographical and stratigraphical range of nikoliviids

UK ENGLAND	Herefordshire	*Nikolivia milesi*	Middle Dittonian
	Welsh Borderland (Mainly Brown Clee area, Turner 1973)	*N.* cf. *balabayi* *N.* cf. *elongata* *N. oervigi* *N. toombsi*	Lower to middle Dittonian
USSR (Karatajute-Talimaa, 1978)	Lithuania	*N. balabayi*? *N. elongata*	Middle Dittonian
	Latvia	*N. balabayi* *N. elongata*	Middle Dittonian
	Estonia	*N. gutta* *N. elongata*	Lower Dittonian
	Brest	*N. gutta* *N. elongata*	Lower Dittonian
	Volini	*N. elongata*	Lower Dittonian
	Podolia	*N. oervigi* *N. elongata* *N. balabayi* *N. elongata*	Middle Dittonian Lower Dittonian

[*Table continued overleaf*]

Geographical and stratigraphical range of nikoliviids (cont.)

CANADA	Mackenzie Mountains, North West Territories (Dineley and Loeffler 1976)	*N.? heintzae*	Transitional, between Delorme Fm. and Road River Fm. Lower Dittonian?
	Canadian Arctic (Vieth 1980)	nikoliviids, including *Canonia grossi*	Lower Devonian
SPITSBERGEN	Dr. Daniel Goujet (pers. comm.)	*Nikolivia* spp.	Lower Devonian
AUSTRALIA	Carnarvon Basin (Turner and Dring 1981) Toko Syncline (Turner *et al.* 1981)	nikoliviid indet.	Lower to Upper Devonian

Abbreviations: BMNH P. British Museum (Natural History), Department of Palaeontology
RSM Royal Scottish Museum, Edinburgh
BU Birmingham University

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REFERENCES

ALLEN, J. R. L., HALSTEAD (TARLO), L. B. and TURNER, S. 1968. Dittonian ostracoderm fauna from the Brownstones of Wilderness Quarry, Mitcheldean, Gloucestershire. *Proc. geol. Soc. Lond.* **1649,** 141–153.

——and TARLO, L. B. 1963. The Downtonian and Dittonian Facies of the Welsh Borderland. *Geol. Mag.* **100,** 129–155.

DINELEY, D. L. and LOEFFLER, E. J. 1976. Ostracoderm faunas of the Delorme and associated Siluro-Devonian formations, Northwest Territories, Canada. *Spec. Pap. Palaeontol.* **18.** 214 pp.

GROSS, W. 1967. Über Thelodontier-Schuppen. *Palaeontographica*, (A) **127.** 64 pp.

—— 1968. Porenschuppen and Sinneslinien des Thelodontiers *Phlebolepis elegans* PANDER. *Paläont. Zeit.* **42,** 3/4, 131–146.

HEINTZ, N. 1972. The thelodont *Sigurdia lata* n.g., n.sp. from the Lower Devonian at Sigurdfjellet, Spitsbergen. *Norsk Polarinstitutt, Arbök*, **1970,** 112–116.

KARATAJUTE-TALIMAA, V. N. 1968. New Thelodonti, Heterostraci and Arthrodires from the Chortkov horizon of Podolia. In *Ocherki po filogenii i sistematike ryb i beschelyustnykh*, 33–43 and 168. [English transl. BLL.]

—— 1978. *Telodonty silura i devona SSSR i Shpitsbergena.* 334 pp. Mokslas, Vilnius. [In Russian.]

KEMNA, A. 1903. Les récentes découvertes des Poissons fossiles primitifs. *Bull. Soc. Belge géol. Bruxelles*, **17,** 339–382.

KIAER, J. and HEINTZ, A. 1932. New Coelolepids from the Upper Silurian on Oesel (Esthonia). *Eesti Loodustead. Arch. Naturk., Estlands*, (1) **10,** 1–8.

MÄRSS, T. 1979. Lateral line Sensory System of the Ludlovian thelodont *Phlebolepis elegans* Pander. *Eesti NSV Teaduste Akadeemia Toimetised*, **28** (Geol. 3), 108–111. [In Russian with English summary.]

——and EINASTO, R. 1978. Distribution of vertebrates in deposits of various facies in the North Baltic Silurian. *Eesti NSV Teaduste Akadeemia Toimetised*, **27** (Geol. 1), 16–22. [In Russian with English summary.]

MILES, R. S. 1973. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder girdle. *Bull. Brit. Mus.* (*Nat. Hist.* (*Geol.*)), **24** (2), 111–213.

ØRVIG, T. 1969. The vertebrate fauna of the *primaeva* beds of the Fraenkelryggen Formation of Vestspitsbergen and its biostratigraphic significance. *Lethaia*, **2** (3), 219–239.

POWRIE, J. 1870. On the earliest known vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone of Forfarshire. *Trans. Geol. Soc. Edin.* **1,** 284–301.

RITCHIE, A. 1963. Palaeontological Studies on Scottish Silurian Fish-Beds. Ph.D. Thesis, Edinburgh (unpubl.).

——1968. *Phlebolepis elegans* Pander, an Upper Silurian thelodont from Oesel, with remarks on the morphology of thelodonts. *In* ORVIG, T. (ed.). *Current problems of Lower Vertebrate Phylogeny*, 82–88. Almquist & Wiksell, Stockholm.

STENSIÖ, E. A. 1958. Les cyclostomes fossiles ou ostracodermes. *In* GRASSÉ, P.-P. *Traité de Zoologie*, **13** (1), 173–425. Masson, Paris.

——1964. Les cyclostomes fossiles ou ostracodermes. *In* PIVETEAU, J. *Traité de Paléontologie*, **4** (1), 96–383. Masson, Paris.

TRAQUAIR, R. H. 1899. On *Thelodus pagei*, Powrie sp. from the Old Red Sandstone of Forfarshire. *Trans. Roy. Soc. Edin.* **39,** III (no. 21), 595–602.

TURNER, S. 1972. Report of research. *Ludlow Research Group Bull.* **19,** 17–18.

——1973. Siluro-Devonian thelodonts from the Welsh Borderland, *Jl geol. Soc. Lond.* **129,** 557–584.

——and DRING, R. S. 1981. Late Devonian thelodonts (Agnatha) from the Gneudna Formation, Carnarvon Basin, Western Australia. *Alcheringa*, **5,** 39–48.

——JONES, P. J. and DRAPER, J. J. 1981. Early Devonian thelodonts (Agnatha) from the Toko Syncline, western Queensland, and a review of other Australian discoveries. *BMR Jl Australian Geol. & Geophys.* **6,** 51–69.

VIETH, J. 1980. Thelodontier-, Acanthodier- und Elasmobranchier-Schuppen aus dem Unter-Devon der Kanadischen Arktis (Agnatha, Pisces). *Göttinger Arb. Geol. Paläont.* **23,** 1–69.

WHITE, E. I. 1935. The ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. *Phil. Trans. Roy. Soc.* (B) **225,** 381–457.

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